Determination of Nutrient Requirements of Forest Stands

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I. Introduction

The extensiveness of the present subject precludes making a complete survey of published work. Instead the reviewer has tried to discuss in some detail the principles of various approaches toward the goal, which is full comprehension of the nutritional situation in forest stands. The references have been chosen, primarily, with the intention of providing instructive examples of the different methods. The reader may find other, equally good examples among the references in the cited papers, particularly in the following reviews or monographic articles: Ehwald (1957), Gessel (1962), Ingestad (1962), Leyton (1958a),

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Ovington (1962), Rennie (1962), Tsutsumi (1962), Wehrmann (1963a), and White and Leaf (1957). Information can also be obtained from the proceedings of the First North American Forest Soils Conference, held in East Lansing, Michigan, in 1958. (A second conference was held in Corvallis, Oregon, in August, 1963.) Special symposia on tree nutrition were held at Duke University in 1959 and in Berlin in 1961 (Fiedler, 1962).

Before we can discuss the methods for determining nutrient requirements of forest trees and stands, we must define or at least discuss the concept "nutrient requirement" and some related terms.

Nutrient requirement or nutrient demand is a physiological concept, implying a living organism with certain activities (growth, respiration, photosynthesis, etc.). When speaking of nutrient demand in a looser sense we mean (or should mean) the nutrient demand for "normal" development of the organism in question—for example, for an average yield of a forest stand. It follows that we should avoid speaking of the nutrient requirements of a *soil* when we mean the nutrient requirements of the crops grown on that soil.

When using the terms in a stricter sense we must indicate for what kind of performance the nutrients are required. It is thus possible to speak of the nutrient requirements for maximum growth of a certain stand, or for a yield of 10 m^3 per hectare, etc. There can be a certain nutrient requirement for flower initiation or for nitrogen fixation by nodule bacteria as well as for growth or photosynthesis. Unfortunately, there are very few cases established in which a mathematical relationship has been obtained between nutrient supply and defined physiological processes in forest stands. As a rule, therefore, we cannot determine the nutrient requirements of forest tree species as strictly as is desirable, but when the term nutrient requirement is used in this paper, it should be read as "the nutrient requirement for a certain growth performance," which will be described more closely where possible. In a few cases we shall also discuss the nutrient requirements for processes other than growth.

Another term of interest in this connection is "nutrient status." The nutrient status of a forest stand is a measure of the degree in which the nutrient requirements for maximum growth are satisfied. A stand with optimum nutrient supply thus has a very good (or optimum) nutrient status, whereas the opposite is true of stands on many poor sites. It is clear that the nutrient status can be optimum or in excess with respect to some plant nutrients at the same time that it is very low in others.

As both nutrient requirement and nutrient status are physiological concepts, they should be determined primarily by physiological methods. Physiological responses of many kinds may be studied quantitatively in relation to the nutrient level in the substrate or in the plant. If the nutrient requirement is measured in relation to the external nutrient supply, we may speak of "external nutrient requirement." On the other hand, the nutrient requirement may also be measured in relation to the internal nutrient level within the plant, in which case it is called the "internal nutrient requirement."

Whether we speak of external or internal nutrient requirement, it is essential to remember that the response curves on which the determinations are based, directly or ultimately, may be of various shapes. Some plants may retain a relatively good growth at external or internal nutrient levels considerably below the optimum, because of the flat shape of their optimum curves. Others may have a narrow optimum range, outside of which the growth rapidly decreases. Different species may also have very different abilities to grow at a certain nutrient supply, not only because of their nutrient requirements for maximum growth but also because of their abilities to extract nutrients from the substrate, and, last but not least, because of their genetically or ontogenetically determined growth potential. A seedling of a tree or a herb may make higher demands on an ample and steady external nutrient supply than a full-grown tree in a stand, or than a perennial plant in a closed community, because of its high rate of growth (in relation to the amount of living tissues).

It is also necessary to have terms that describe the soil with respect to its ability to supply plant nutrients. We can here, in the first place, recognize as an intensity factor the actual concentration of plant nutrients in the soil solution. The capacity factor is, however, often more important in soils in which a considerable part of the plant nutrients occur as adsorbed ions or in even less available forms (for example, organic nitrogen and phosphorus or potassium and ammonia fixed in clay minerals). It is of course possible to speak of nutrient concentrations or levels in the soil, or of nutrient availability, but such data are meaningless except in connection with some information on the method of determination. The term "nutrient supply" is used here in a rather unspecific way to cover the general concept of nutrients furnished in an available form by the site to the plants, regardless of the degree to which these nutrients are utilized by a certain crop.

As will be discussed later, these various aspects of the problem of

nutrient requirements are of great importance with regard to both the application of physiological findings to ecological conditions and the possibilities for comparing the nutrient demands of various species and strains (cf. also Ingestad, 1962).

II. Various Approaches in Forest Nutrition Research

A. Different Methods for Assessment of Nutrient Status and Nutrient Requirements, Their Advantages and Drawbacks, and the Nature of the Information Obtainable with Each

Most forest nutrition work includes the use of one or more of the techniques listed below. These are discussed separately in this section. Section II,B is devoted to a discussion of various combinations of the different methods. The commonly used techniques are the following:

1. Experimentation in forest stands.
2. Experimentation in culture experiments (pots, solution culture, nurseries, forest plantations).
3. Soil analysis.
4. Diagnostic plant analysis and visual symptoms of deficiency and excess.
5. Indicator plant methods: (*a*) phytosociological methods; (*b*) methods using indicator plants as extractors of nutrients from the soil.
6. The substitution principle (use of the total nutrient consumption of a crop as a measure of nutrient demand).

1. EXPERIMENTATION IN FOREST STANDS

It is, as a rule, easier to add more nutrients than to cut down the natural supply. The latter can seldom be done without serious changes in water regime and other factors. The standard treatment is thus application of plant nutrients in a form available to the plants—that is, fertilization. The fertilizers can be applied to the ground, broadcast as solid substances, watered on in solution (Hesselman, 1937), or injected into the soil in gaseous form (ammonia, see Mayer-Krapoll, 1956; Zöttl and Kennel, 1963). The application can be combined with soil working. The fertilizers can be put on in spots or in furrows or can cover the whole ground. The nutrients can also be supplied directly to the trees by spraying or dipping the foliage (Wittwer and Teubner, 1959; Shibamoto and Nakazawa, 1960; further references in Table II) or by injection into the stem (Roach and Roberts, 1945; North, 1962; see also Table II). In any case it is essential that groups of control trees receive exactly the same treatment as the fertilized trees, except for the nutrient application.

The effect of the treatment can be measured as growth (total growth, or more conveniently, stem volume increment, height growth, or diameter increment) or as changes in some other physiological process, such as flowering or fruiting (Chandler, 1938; Steinbrenner *et al.*, 1960). For agricultural crops even transpiration has been used in the so-called "Anwelkmethode" (Arland, 1955).

The following points merit particular attention when field experiments are designed:

1. The questions to be answered by the experiment should be clearly formulated and be as simple as possible, the latter mainly because of the necessity of keeping down the total area of the experiment to a reasonably uniform area (because it is often difficult to find large, uniform areas in a forest).

2. The questions posed should be pertinent to the subject. It is, for example, of little value to design an experiment with phosphates of different solubility in a stand with predominating deficiency in nitrogen. When nothing is known beforehand about the nutritional situation, so-called minus experiments are often the best approach. At a somewhat later stage when something is known about which nutrients occur in growth-limiting amounts, factorial experiments are to be recommended.

3. The experimental design must be statistically sound. Thus, plots should be randomly assigned, at least in duplicate for each treatment. On the other hand, it is not absolutely necessary to discard all earlier experiments which do not fulfill these requirements. Often the results of several separate experimental series with similar designs can be dealt with together (e.g., Wiedemann, 1932; Mitchell and Chandler, 1939; Hausser, 1953; Hausser and Schairer, 1953; Mitscherlich and Wittich, 1958; C. O. Tamm and Carbonnier, 1961). In cases where the trees have distinct annual rings, diameter growth in a plot can be studied in relation to earlier growth as well as in relation to growth on adjacent plots (Fig. 1), a circumstance that greatly increases the precision of stem growth measurements. A sufficient number of sample trees is required for all types of measurements. In the case of pine or spruce stands in Sweden, it has been calculated by Matérn (in Carbonnier, 1962) that a determination on 25 sample trees from each of two duplicate plots would yield a standard error for the difference in relative growth between two treatments, measured on increment cores, of 6% to 7% of the control treatment growth. If the expected growth difference is 25%, this would allow fairly safe conclusions.

4. Wherever possible it should be ascertained that a certain treatment has the desired effect, and no important side effects. A fertilizer broadcast on the ground may never reach the tree roots in any significant amount because the ground-cover vegetation may utilize most of it, or because it is rapidly transformed into an unavailable form in the soil (for example, iron or manganese in alkaline soils), or because of an unfavorable water regime (such as summer drought combined with excessive winter leaching). The indirect effects of fertilizer applications are even more difficult to interpret. It has long been recognized that the

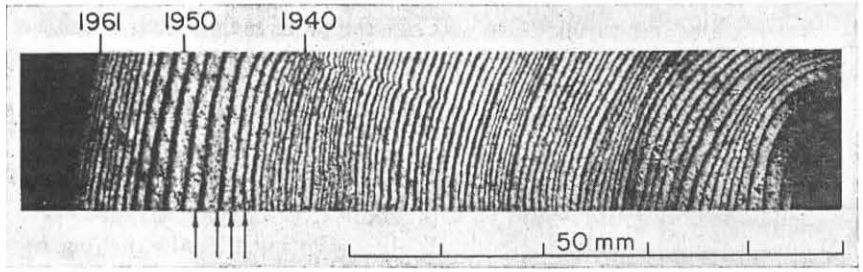

FIG. 1. Annual growth rings of a pine growing on an outwash sand plain in southern Norway. Each arrow indicates an addition of 100 kg of nitrogen per hectare (as calcium nitrate). See Brantseg (1962a).

effects of lime application are indirect in most cases as far as higher plants are concerned. Similar indirect effects may also follow fertilization with phosphates and some types of nitrogenous fertilizers (ammonia, urea, etc.), which may affect the microflora and soil fauna. If a nutrient that is limiting for growth of both higher plants and microorganisms is supplied, the demand for other nutrients may increase, and it is possible that the supply may temporarily become inadequate. Even applications of gypsum (also a constituent of superphosphate), which has been reported to increase growth in some early experiments both in agriculture and forestry, may change the nutrient availability. The slow release of calcium and sulfate ions may, by ion exchange, increase the nutrient concentration in the soil solution for a longer or shorter period; characteristically in many forest soils this concentration is extremely low, and most plant nutrients occur as adsorbed ions. Many forest plants, including some trees, are sensitive to certain ions or compounds and may therefore be damaged or killed by higher doses of fertilizers containing, for example, chlorides or cyanamide. Liming kills reindeer moss and other lichens as well as *Sphagnum,* and copper or zinc salts in relatively

low concentrations may also kill both mosses and lichens. The importance of all these "secondary" fertilizer effects should not be exaggerated, but they should be observed and reported. It is also desirable to try other ways of supplying the trees with the same nutrient if a soil application of a certain fertilizer has profound side effects. Foliar spraying or dipping and stem injections may in many cases be useful in making qualitative tests. The uptake of an added nutrient can be followed by plant analysis, most accurately by means of radioactive tracers. (Schönnamsgruber, 1955; Witherspoon *et al.,* 1962).

A positive reaction to an added nutrient by the sample trees can usually be taken as evidence for a deficiency of that nutrient; the exception would be where important indirect effects can be suspected. The absence of a reaction is also evidence, although it is not very conclusive. To establish the nutrient status more accurately, dosage experiments that contain at least optimum supplies, and preferably supraoptimum supplies, are required. Experiments in forest stands can also give information on the behavior of different species (Mitchell and Chandler, 1939), but it should be recognized that factors other than nutrient requirements (for example, rooting habits, shading, and in short-term experiments degree of growth predetermination) may well contribute to the differences found in growth responses after fertilization.

In the literature there are numerous reports of cases in which organic substances of various types have increased forest growth. Instances have also been reported in which soil working or trenching has improved regeneration and growth of young trees. Treatments of this kind are, as a rule, not suitable for use in investigations on nutrient requirements. Their effects are too complex, affecting microbiological conditions as well as soil chemical and physical properties. But they must be mentioned here, because in many earlier experiments (Galoux, 1954), and occasionally in more recent ones (Hausser, 1960), the fertilizer application was combined with soil working and/or humus displacement. It is then not always clear how much of the effect should be ascribed to the fertilizers and how much to the other treatments. Even irrigation experiments may have such a double effect (Holmbäck and Malmström, 1947; Brantseg, 1962b). It should be noted also that some commercial fertilizers contain magnesium, sulfur, or trace elements in addition to the major nutrient elements. Therefore, special attention must be given to the choice of fertilizers, if the effect of the various nutrient elements is to be assessed correctly on sites where deficiencies in elements other than nitrogen, phosphorus, and potassium can be suspected.

2. CULTURE EXPERIMENTS

The technical difficulties in experimentation in forest stands have led many workers to a more physiological approach, experimenting with seedlings or young trees under laboratory conditions, in nurseries, or even in small field plots. Some of the obvious advantages of such methods are: (1) More complicated experimental designs can be used without prohibitive costs, because of the possibility of preparing a homogeneous substrate and of keeping down other sources of variation in growth, including those of genetic origin. (2) Much time can be saved by using seedlings or young transplants in experiments over a limited time. (3) There are greater possibilities of evaluating total growth and growth response in more detail than in experiments in forest stands. (4) Most of the possible indirect effects of fertilizers can be entirely eliminated in solution culture and to a large extent also in soil culture in pots.

The other aspect of this approach is that it may give excellent information on the nutrient physiology of seedlings or young trees, but not necessarily on the behavior of more mature trees under natural conditions. The internal nutrient requirements of seedlings may be different from that of adult trees because of differences in anatomy and cell physiology. Even where this factor is of minor importance, however, there are differences in the way in which a certain internal nutrient level is established. An example is potassium deficiency in Norway spruce, where the visual symptoms differ considerably between seedlings and more mature trees (Ingestad, 1962); the explanation may be sought in differences in potassium reserves within the plant in relation to growth rate.

Further differences between trees in the forest and small plants in pots or in water culture are the differences in mycorrhizal and rhizosphere organisms, which may have a considerable influence on nutrient uptake. Still more important, however, is the fact that a soil sample in a pot may be ecologically very different from the same amount of soil *in situ* in the forest. This difference, which is also discussed in Section III,A, has its causal background (1) in the different physical conditions (including water regime) prevailing in a pot as compared with those in a field plot, and (2) in the intimate biological relations between tree roots, mycorrhizal fungi, and substrate in many soils. These relationships are also important for the interpretation of some types of soil analysis (see below). In the case of pot culture experiments it must be kept in mind that the results are not immediately applicable to field conditions.

3. SOIL ANALYSIS (INCLUDING SOIL WATER ANALYSIS AND SOIL INCUBATION EXPERIMENTS)

Chemical analysis of the amounts of plant nutrients in the soil is certainly of great interest in forest nutrition studies. The soil is the main source of nutrients to the trees and also to most other forest plants, and the soil nutrient supply is often a limiting factor for forest growth. A difference in soil nutrient concentrations and/or total available amounts per unit area between stands with different yields may often be the cause of that yield difference. Very often several soil factors, both physical and chemical, are interrelated, and the choice of one or a few of these factors for correlation studies may be risky. Multiple correlation studies, now greatly facilitated by electronic computing machines, remove some of the worst pitfalls, provided that the parameters used are good expressions of the more important factors operating (Fig. 2; Dahl *et al.*, 1961). However thorough the statistical analysis, it should be borne in mind that a correlation itself, even if highly significant, is no proof of a direct causal relationship.

The first question to be considered in connection with soil analysis for plant nutrients concerns the method of extracting the nutrients in question. We can choose among total analysis (including silicate-bound mineral nutrients) and assay of hydrochloric acid-soluble nutrients; determination of nutrients extractable with weaker acids, buffer solutions, or water; measurement of total exchangeable ions; or measurement of ions absorbed by ion-exchange resins mixed with the soil (Williams, 1962; Madl, 1960). Test plants can also be used as nutrient extractors (see below under Section II,A,5,b). If a method is chosen that extracts only a small part of the total amount in the soil, a part believed to be more available to the plants than the rest, it must be remembered that this amount represents the difference between what is being released from litter and minerals (and fertilizers) and what is being removed by roots and by leaching over a period of time. Under certain circumstances other processes may also influence this balance (atmospheric nutrient supply, nitrogen fixation by organisms, fixation of potassium and ammonium ions in clay minerals, denitrification, etc.). Changes in the amount of, say, nitrate nitrogen in the soil may thus be caused either by changes in rate of litter breakdown and nitrification or by changes in consumption of nitrate or ammonia. It is thus natural that important seasonal changes occur in the contents of ammonia and nitrate in forest soils (Tjulin, 1954, 1960; Vinokurov and Tyurmenko, 1958; see also Handley, 1963).

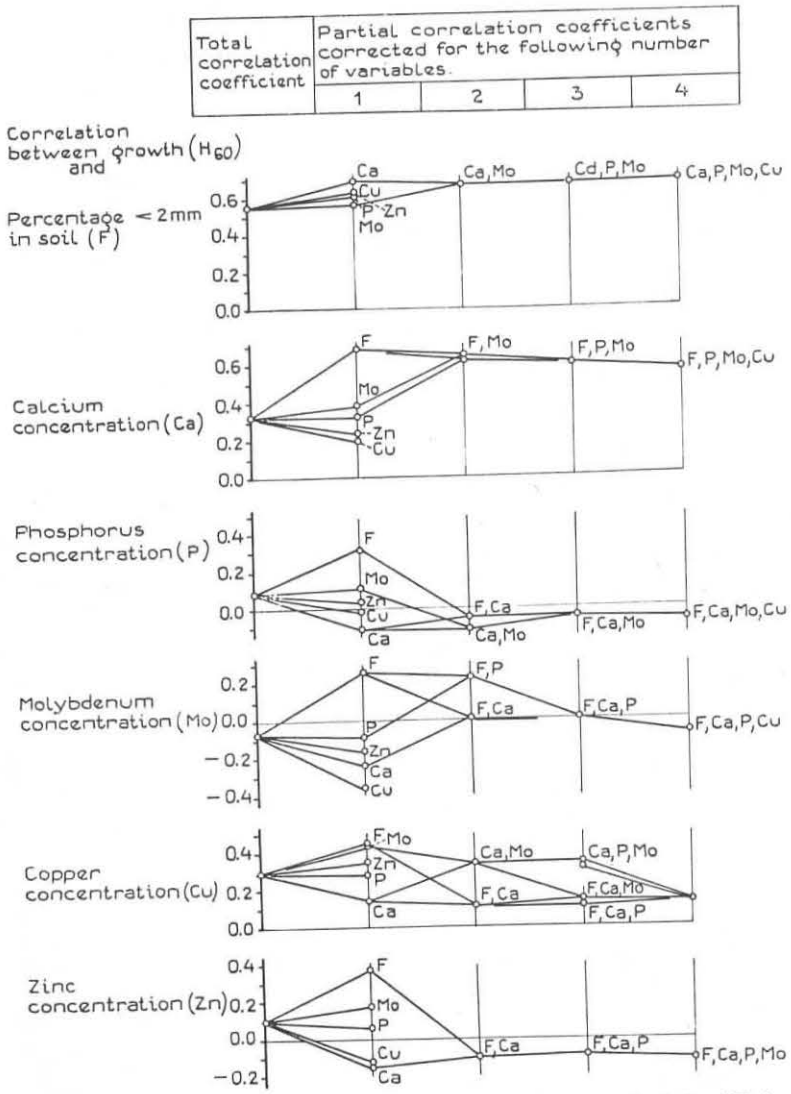

FIG. 2. Single and multiple correlation coefficients between site-index (H_{00}) and soil properties in *Pinus sylvestris* stands in Finland. From Dahl *et al.* (1961).

The difficulties arising from the dynamic character of available nutrients in the soil have led many investigators to make soil incubation experiments rather than direct extractions. Good correlations have been established between released nitrogen, on the one hand, and seedling growth and forest humus type (Hesselman, 1927) or tree yield and foliar nitrogen concentrations (Zöttl, 1960), on the other (Fig. 3). It is

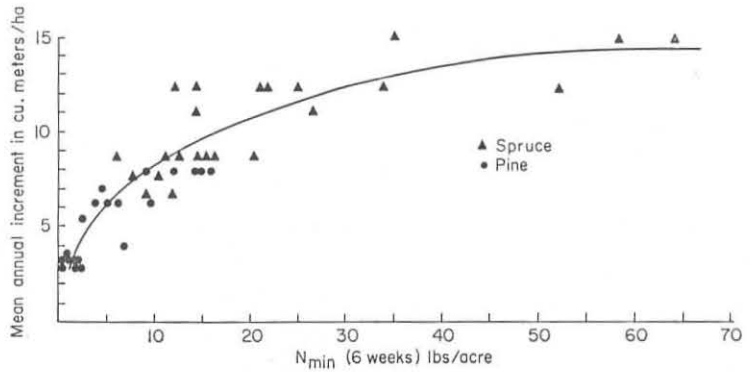

FIG. 3. The relation between the mean annual increment of Bavarian spruce and pine stands and the amounts of mineralized nitrogen in the humus layer. From Zöttl (1960).

thus evident that short-term incubation tests on ammonia and nitrate formation in soil samples may provide important information. Yet it is not clear how general the conclusions are that can be drawn from such experiments, or to what extent it is possible to make quantitative calculations of nitrogen mobilization from them.

A soil sample in an incubation flask is something very different from the same soil *in situ*, not only because of other temperature and moisture conditions, but also because of the dependence of the soil microflora on living roots. Competition for nutrients between roots is, of course, eliminated in the flask. Even more important may be the fact that easily decomposable organic matter is suddenly released by the death of roots, mycorrhizal fungi, and rhizosphere organisms (Romell, 1935). It is often found in incubation experiments with forest humus that the rate of nitrogen mobilization follows a sigmoid curve (Cunningham, 1962), slow at first (or even with a lag phase in so-called inactive mor), then increasing, and later on (after about a year) slowing down again. The final mobilization may be one-fourth or more of the total

amount of nitrogen present in mor samples. Liming increases nitrification, but in long-term experiments Romell and Viro found decreased total nitrogen mobilization in some soils (see Viro, 1963). Forest mull samples, like arable soils, would be expected to change their biological activity less than mor on sampling, because more of the bacteria and other decomposing organisms survive the sampling. Yet Zöttl (1960) obtained much better correlation between incubation data and foliar nitrogen levels with mor than with mull, thus demonstrating the value of the method, even if our understanding of its background is not quite clear.

An intensely growing forest stand may almost exhaust the soil supplies of easily soluble nutrients before growth ceases. This seems to be the explanation of the negative correlation found by Holmen (1964) between forest yield and soil contents of ammonium lactate-soluble phosphate (and potassium) on a drained peatland, where total phosphate showed the opposite trend (Fig. 4). Peat often has extremely small supplies of both total and easily soluble phosphate and potassium.

Other important questions in connection with forest soil analysis are the following: Which horizons should be analyzed, and should the results be expressed on a weight or a volume basis or as amounts per unit area? No definite answer can be given here to either of these questions. It seems important that the main rooting zone should be sampled most thoroughly, with some consideration given also to lower horizons as long as they contain roots to any notable extent. But with such rules, less than 2 or 3 decimeters of soil will be sampled in many subarctic coniferous forests, whereas root penetration on good sites in better climates may extend over several meters. In fact, there is often a trend toward deeper profiles and consequently deeper rooting with increasing site fertility; it is essential, therefore, that sampling to a standard depth be combined with descriptions of root distribution and profile characteristics.

The other question, regarding a weight, volume, or area basis, is very important in certain cases, for instance when organic and mineral soils are compared. In studies of soils with comparable volume-weight ratios it may sometimes be permissible to omit volume determinations and thus avoid complicating sampling further than necessary to ascertain comparable samples. It has been recommended that forest soil values should be expressed on an area basis "unless previous experience justifies simpler methods" (Gjems *et al.*, 1960). The multiple regression analysis by Dahl *et al.* (1961) (see Fig. 2) suggested that pine site class in Finland was positively correlated with the amount of soil material of

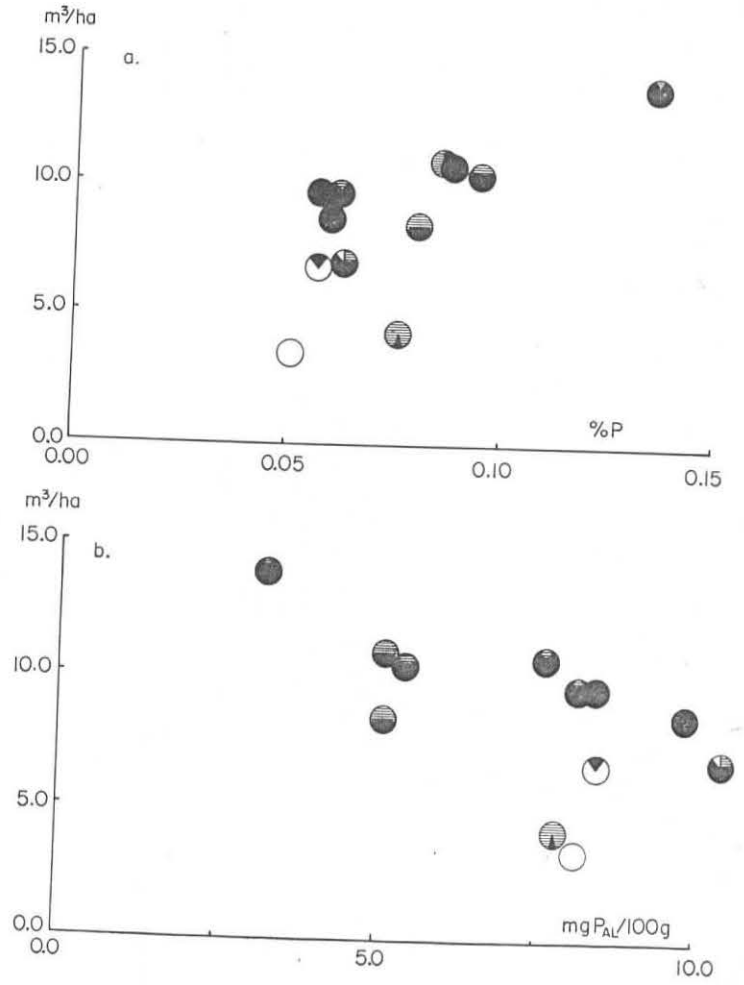

FIG. 4. Current growth on twelve plots of drained peat land in eastern Sweden, plotted versus the concentration of (a) total P (%P) and (b) ammonium lactate extractable P (P-AL) in the layer 0 to 20 cm. The sectors of each dot are proportional to the percentages of spruce (black), pine (white), and hardwoods (hatched). The plots dominated by pine and hardwoods are somewhat less well drained than the spruce dominated plots. From Holmen (1964).

less than 2-mm particle size and with the concentration of EDTA-soluble calcium in this material. Introduction of the amounts of various ions instead of concentrations tended to obscure the relationships. Total P determinations have been found useful as indicators in the Netherlands (van Goor, 1956a) and in Australia (Baur, 1959). Heiberg *et al.* (1959) found exchangeable potassium concentrations well correlated with tree growth, but van Goor (1956b) preferred the concentration of hydrochloric acid-soluble potassium. On the other hand, there is considerable evidence supporting the use of total nitrogen per unit area as an important site characteristic (Romell, quoted by C. O. Tamm and Carbonnier, 1961; Zinke, 1960; Heilman and Gessel, 1963b).

The substrate for forest trees always contains water, and it is thus in principle possible to correlate forest growth with the composition of the soil solution, either expressed under pressure, collected in lysimeters, or sucked up from the ground water. It is evident, but somewhat outside the scope of this paper, that water chemistry must be of great importance for extremely wet forests, such as mangrove or cypress swamps.

Like soil chemical composition, water chemistry is also related to forest growth (Troedsson, 1952), and several authors have emphasized the "flush effect" (e.g., Gorham, 1953). A direct evaluation of the flush effect implies estimates of the amounts of nutrients taken up from the seeping water. Such measurements are difficult, even with isotope techniques, because some of the more important plant nutrients (nitrogen, sulfur, and phosphorus to the limited extent that this element is translocated) are moving partly in the form of organic compounds of unknown composition. Heavy metals would be expected to move as chelates. As a substitute for direct measurements of uptake from "moving ground water," data on the composition and rate of movement of the water are of interest (Troedsson, 1952).

The soil characteristics best correlated with forest nutrition are not necessarily determined by particular fractions of the soil nutrient supply. We have already mentioned the possibility of total analysis. Forest trees are long-lived, and their root systems may be capable of extracting more nutrients from soil minerals than are those of agricultural crops, not so much because of higher efficiency as of longer persistence. The growth of pine forests on sandy soils has been found to depend on the mineralogical composition of the sand both in southern Sweden (O. Tamm, 1937) and northern Germany (Wittich, 1942; Ehwald and Kopp, 1962). The mineralogical composition can be expressed as per cent quartz in relation to the per cent of other minerals of greater nutritive value. For

certain soils—for example, noncalcareous sandy soils on the Fennoscandian shield—a simple method based on separation according to specific gravity has proved very useful (O. Tamm, 1937). It seems likely that, in the future, determination of the mineralogical composition of the clay fraction may be of interest from the forest nutrition point of view.

Even in cases where forest growth apparently depends on the general fertility level in the soil, a better correlation may be obtained between certain unspecific soil properties than with soil nutrient contents. Such properties are acidity, exchange capacity, "base-saturation," and the conductivity of the soil solution. The exchange capacity is a measure of the soil's ability to store cations, but it is a function of physical as well as chemical properties. The pH and the degree of base-saturation both give information on the proportions between acid groups and cations other than hydrogen ions in the soil. These variables have a great influence on both plant growth and nutrient turnover in the soil (Sjörs, 1961). It is thus not surprising that pH and base-saturation under certain circumstances give good correlations with forest growth; it must be remembered, however, that the causal relationships behind these correlations are very complex and include factors not directly connected with nutrition.

The conductivity of the soil solution (adjusted to a standardized proportion between soil and water) can also be correlated with forest growth (Arrhenius, 1957). As the dominating metallic cation in the soil solution in humid soils is, as a rule, calcium, this correlation gives somewhat similar information to that found in the case of EDTA-extractable calcium (Fig. 2). Conductivity can also be of considerable value in distinguishing supraoptimum salt concentrations in saline or irrigated soils.

Information on the chemical and physical properties of soil parent material as obtained from geological maps may also help in the understanding of the site nutrient regime. The rapidly increasing knowledge of the relations between soil profile types and soil chemistry in many areas is an even more important source of information, but a detailed discussion of this theme belongs to the subject "site classification." Here only one example will be mentioned of how soil data can be used to construct mathematical expressions, "scalars," apparently correlated with nutrient regime. Loucks (1962) studied soils and forest stands in eastern Canada and used nomographical methods to combine four independent sets of data into one "synthetic nutrient scalar," well correlated with, for example, the growth of balsam fir. Loucks' original observations in-

cluded the depth of the A horizon (expressed as A_1 minus A_2), depth of solum, silt and clay content, and a "run-off scalar" (a function of topography). In further sections Loucks also uses "a synthetic moisture scalar" and a "synthetic local climate scalar." Topography is of course important for both these "scalars"; soil texture is included in the "moisture scalar" as well as in the "nutrient scalar."

It is to be expected that approaches similar to that of Loucks will be more common in the future; the use of electronic computers greatly facilitates the construction and use of various types of indices. Of course it is also possible to incorporate chemical data in the indices. The present author finds no disadvantage in this type of work, as long as it is remembered that the investigation is purely empirical and statistical. Even if well-known physiological relationships have been used for the construction of the indices, it must be verified in each case that a combined variable really offers some advantage over a simpler approach. Examples of both the risks and the advantages of combined "indices" can be taken from the field of bioclimatology.

4. DIAGNOSTIC PLANT ANALYSIS AND VISUAL SYMPTOMS

The soil supply of nutrients affects plant growth indirectly through its effects on the internal nutrient level in the plant. Therefore, a natural way around the difficulties involved in soil analysis is to determine the internal nutrient concentration in the plant, and consider it as an integrated result of soil nutrient availability and physiological uptake (Lundegårdh, 1951). More extreme conditions with respect to various elements often show up not only as extremely high or low concentrations of the element in question but also as more or less specific morphological abnormalities, "deficiency symptoms" or "toxicity symptoms," which also can be used in forest nutrition studies.

a. Chemical Analysis. An unequivocal relationship between growth and the nutrient concentration in the analyzed organ is the first physiological prerequisite for diagnostic plant analysis. It is also implied that a positive correlation exists between internal nutrient level and the external level. Very often these relationships are taken for granted without control experiments, or those experiments that are carried out deal with only some of the possible interactions. Several factors other than nutrient supply are known to affect nutrient concentrations and deficiency symptoms in the tissues of woody plants. The greater part of this section will be devoted to a discussion of such influences and the technical possibilities of avoiding errors in the interpretation of data. Most of the discussion of foliar analysis in forest nutrition work will follow in Sections II,B and III,B.

Factors of importance in diagnostic analysis are: (1) age of sampled organ (White, 1954; Höhne, 1963a; Wells and Metz, 1963), (2) season (Mitchell, 1936; Olsen, 1948; Leyton, 1948; Schönnamsgruber, 1955; White, 1954; for seasonal dry weight changes in needles see Rutter, 1957; C. O. Tamm, 1955), (3) position in crown (Leyton and Armson, 1955; White, 1954; Zöttl and Kennel, 1963; Höhne, 1963a), (4) shading (Müller, 1934; van Goor and van Laar, 1958; Manabe, 1961), (5) fruiting (Gessel, 1962; Strebel, 1960), (6) weather conditions prior to sampling, particularly drought and rain leaching (see below), (7) time of day (Bolle-Jones, 1957), and (8) attacks of parasites (Kirkpatrick *et al.*, in press; cf. Rennerfelt and Tamm, 1961). Adhering dust particles may also act as a source of error, particularly in iron analyses (Mason, 1953; Nicholas *et al.*, 1956), and in industrial areas special precautions have to be taken against pollution.

Some of the disturbances listed above can be avoided by a careful standardization of sampling. It seems to be commonly agreed that evergreen temperate-zone conifers should be sampled after the end of the growing period and that deciduous trees should be sampled 2 to 3 weeks before autumnal yellowing (Leyton, 1958a). Regarding the position in the crown, most authors recommend sampling twigs as near the tip as possible, and in conifers current needles from a particular whorl (White, 1954; Zöttl and Kennel, 1963); some authors have, however, found that low and shaded leaves may be better indicators of nutritional differences than sun leaves (Shorrocks, 1961; in *Hevea*). Where morphologically different short shoots and long shoots occur together, it seems advisable to sample one type only, preferably leaves at a certain developmental stage. In the case of tropical forest trees no information seems to be available on seasonal variation, but the importance of a sampling standardized with respect to position in tree and rainy seasons has been studied for the oil palm and rubber tree (Prevot and Ollagnier, 1954; Ferwerda, 1961; Shorrocks, 1961).

Leaf composition usually seems to reflect nutrient status better than does the composition of other organs (Lundegårdh, 1951; Ingestad, 1962). In certain crops, however, petioles are preferred to leaf blades. For practical purposes, the choice of object is often a matter of convenience and not a question as to which organ is theoretically best. For rubber trees both bark and latex analyses have been tried, although with moderate success (Bolle-Jones, 1957; Shorrocks, 1960). It has been

shown that wood, bark, twigs, and needles all change their composition after fertilizer applications (Heilman and Gessel, 1963a; C. O. Tamm, in press, a). Will (1962) suggests wood and phloem analyses for diagnosing phosphorus deficiencies in *Pinus radiata*. Work correlating wood nitrogen concentrations with various factors is now going on in the writer's laboratory. It is known that root sap varies in composition with the position of the root in the soil (Dimbleby, 1952; Ladefoged, 1948). Bollard (1953) has discussed tracheal sap composition in relation to apple tree nutrition.

Perfect standardization of sampling is, however, no guarantee that foliar concentrations will reflect nutrient status unambiguously. Nutrient uptake and nutrient translocation in the plant represent only part of the processes determining nutrient concentration in a tissue. The most important other process is growth. If growth increases more than nutrient uptake, the result will be lower concentrations (a "dilution effect," Lundegårdh, 1951). Such a dilution or "false antagonism" is often observed if the concentration of one plant nutrient is varied (Ingestad, 1962; C. O. Tamm, 1956a). Steenbjerg (for references see Steenbjerg and Jakobsen, 1963; cf. also Hewitt, 1957) has observed a similar effect in the concentrations of a nutrient when the supply of the *same* nutrient is increased from extreme scarcity to optimum; in most cases the effect was observed only within the range of strong deficiency and when mature cereal plants were analyzed. Phenomena analogous to the "Steenbjerg effect" have also been described for forest trees (Ingestad and Jacobson, 1962; Wittich, 1958; C. O. Tamm, in press, a).

According to the reviewer's opinion, it would be possible to avoid much of the undesirable disturbances due to the typical "Steenbjerg effect" by a meticulous choice of objects for sampling. There is, however, an interplay between growth, growth predetermination, and nutrient supply which is very important in the interpretation of tissue analysis data. The "Steenbjerg effect" is only a special case of this complex problem, which is best explained by an example. In many trees—for example, *Picea abies* and *Pinus sylvestris*—the growth of the current season is largely determined by conditions the year before. The immediate effect of a fertilizer application is then an increase in tissue concentrations. In the next year growth increases, but the uptake may not keep pace (if water-soluble salts were added, they may have been leached away by that time). The result, under certain circumstances, may then be a lowering of the tissue nutrient concentrations in the fertilized trees below those in the unfertilized trees (C. O. Tamm and Carbonnier, 1961, Fig. 13).

Some of the disturbances discussed above may be minimized by a proper choice of reference basis for the analytical data. Most authors report their analyses as per cent of oven-dry weight, and at present there is no reason to abandon this practice. The question is whether other reference bases may supply additional information. Earlier it was common to report percentages of ash (Aaltonen, 1950) or percentages of the sum of certain elements believed to be more important than others (Lagatu and Maume, 1924). Such relative data are less dependent on dry-weight changes in the analyzed organ, and this is an advantage. Several authors (e.g., Leyton 1957, 1958b) have tried to use the ratios between various elements (percentages or milliequivalents per 100 gm) instead of, or together with, dry-weight percentages. Some of these ratios have a certain physiological meaning; K/Ca, K/Mg, and Mg/Ca are, for instance, expressions of antagonism between the cations in question. Quotients like K/N or P/N may signify (at least within suboptimum nitrogen levels) the concentrations of K or P in relation to the amount of protoplasm. In other cases the meaning of such quotients is more or less obscure, and then the interpretation of correlations between growth and various quotients may meet with difficulties.

A further possibility is expression of data as the amounts of nutrients per 100 needles, per unit leaf area, or similar units (Müller, 1934; Leyton, 1954, 1957; Zöttl and Kennel, 1963). This method counteracts the dilution effect, and beautiful correlations may be obtained between growth and needle data; but it must be recognized that the amount of something per 100 needles includes an expression for tree vigor—the weight of 100 needles (cf. Wehrmann, 1959)—and that the various measures of tree growth and vigor are much more closely correlated than growth and nutrient concentrations (C. O. Tamm, in press, a). Results expressed on a unit leaf area basis may be less influenced by variations in vigor, but they are much affected by shading.

It would also be of some interest to test more systematically the nutrient concentrations per unit of *fresh* water-saturated plant material instead of dry, because the (water-saturated) fresh weight is an expression of the volume of cells and cell walls at full turgor, which in mature organs is a more constant property than dry weight. It is particularly in detailed studies of the seasonal variation in nutrient concentrations that the fresh weight (or water) basis might prove useful. Langlet's (1937) investigations have indicated a remarkable diagnostic value of the percentage of dry matter in water-saturated conifer needles in connection with provenance tests and winter survival. Of course there are

technical difficulties involved in the use of a fresh-weight basis instead of dry weight; potassium and other constituents may be lost by leaching, and the respiration losses in samples that are not rapidly dried can be very considerable in certain species, a circumstance that also requires attention where only percentages of dry weight are used (White, 1954).

Assuming that the sampling technique has been standardized with respect to season, organ to be sampled, and sample treatment, we still have to determine the suitable number of sample trees. This number depends on the variability in composition within and between similarly treated trees and on the desired level of accuracy. Recently several investigators have published their experiences regarding this variability in a way that makes them directly useful for the determination of the necessary number of samples (C. O. Tamm, 1956a; Strebel, 1961; Wehrmann, 1963a; Höhne, 1963a). On the other hand, many authors have based conclusions on samples from a small number of trees from each plot, without any information about the within-plot variation. According to C. O. Tamm (1956a), a composite sample of leaves from one branch from each of ten similar pines, spruces, or birches, growing on a uniform sand plain, would yield standard deviations in the dry-weight percentages of nitrogen between 2% and 4% of the values, in phosphorus between 2% and 6%, in potassium between 5% and 7%, and in calcium between 5% and 10%. If a higher accuracy is desired, sampling more trees is preferable to sampling more branches from each tree, because the variation between trees is considerably higher than within trees (if similar branches are chosen). Apparently very few conclusions can be drawn from analyses of a small number of felled sample trees; yet some information can be obtained on the changes from year to year even from a few trees, if the same trees are sampled regularly (C. O. Tamm, 1956a).

It follows from the preceding discussion that the sampling technique must allow sampling of a sufficient number of trees without prohibitive costs in established stands. A man on the ground can cut branches up to a height of 8 to 10 m by means of pruning shears on a pole. Felling is as a rule excluded on permanent plots, so some other method must be resorted to in the case of tall trees. Climbing by ladders or "tree bicycles" is time-consuming; moreover it may be difficult to reach well-exposed branches in the top of the crown. A shotgun may in many cases be the only practical solution (Mitchell and Chandler, 1939). This method works well, particularly with a narrow-bore shotgun and not too small shot (3-mm diameter for spruce and birch). The main disadvantage is that it is difficult to choose particular twigs for sampling. The evidence is somewhat conflicting regarding the variation in composition between various branches in the tops of older trees (Strebel, 1961; Zöttl and Kennel, 1963). The author has obtained good agreement between different samples from the same trees by this method.

Before we come to the interpretation of the leaf analyses made on samples collected with due attention to all sources of errors considered above, we must discuss the variation in leaf composition from year to year in the same stand. There is, under some circumstances, a considerable difference in the levels of certain elements in different years (Plice, 1944; C. O. Tamm, 1954, 1956a; C. O. Tamm and Carbonnier, 1961; Wehrmann, 1961, 1963a). Remezov (1961) has found large variations in litter fall and composition from year to year. Wehrmann ascribes much of the variation in nitrogen concentrations to the depressing influence of drought on soil nitrogen mobilization. A relationship between soil moisture regime and nitrogen regime seems to exist (cf. Fig. 5), but stands annually fertilized with large amounts of nitrogen also show variation (C. O. Tamm, in press, a, b). Rain and drought may also affect leaf nutrient concentration more directly than by changing soil turnover. Some nutrients, potassium in particular, are easily leached from the leaves (Madgwick and Ovington, 1959; Tukey and Tukey, 1962). The intensity of the transpiration stream may affect nutrient uptake (Scott-Russell and Barber, 1960). It is thus still an open question as to what extent the variation in leaf nutrient concentrations from year to year is an expression of a varying nutrient status (defined as responsiveness to nutrient application), and to what extent it should be considered simply as a source of error. In any case there is much in favor of the recommendation of Wehrmann (1963a) to sample stands in more than one year.

Regarding the interpretation of data obtained from leaf analysis (or other types of tissue analysis), we have already mentioned that some authors have found relations between leaf data and site index or other stand properties. Figure 5, taken from Wehrmann (1959), is an excellent example of the relations obtainable, and at the same time it demonstrates the difficulties of interpretation. There is apparently an interaction between soil-water regime, nitrogen supply, and tree growth. Statistical correlations of the type demonstrated in Figure 5 are the only results obtainable, as long as we do not know anything about the physiological meaning of the leaf nutrient levels found. A positive relationship between site index and a leaf nutrient concentration is a challenge for

further research (especially if the partial correlation is statistically significant). A negative correlation may suggest that the nutrient in question occurs in excess, or that some other factor determines the amount of growth and thereby the "dilution" in the plant of the studied nutrient (Nebe, 1962; cf. also the "Steenbjerg effect"). Absence of a correlation must not be taken as evidence of a lack of causal relationships between a nutrient and growth; it is equally possible that the factors described above balance each other.

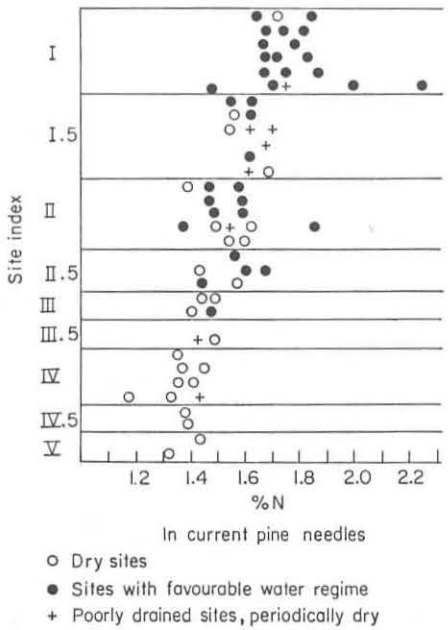

FIG. 5. The relation between site index and foliar nitrogen concentration in Bavarian *Pinus sylvestris* stands. From Wehrmann (1959).

The inference derivable from a strictly nonexperimental leaf analysis investigation is thus limited. The prospects are much better if the leaf data from the studied plots can be compared with leaf data from experimental material, as is described in Section II,B.

Further chances for development of diagnostic tissue analysis may be found in fractionating the organic and inorganic compounds in the plant. It is a well-known fact that a lack of plant nutrients may cause disturbances in metabolism, followed by accumulation of, for example, asparagine (Steward *et al.*, 1958). Some of these effects may be specific enough for diagnostic purposes (Kessler, 1961). Moreover, part of the nutrients in the plant may be inactivated and therefore without influence on metabolism (for instance, iron precipitated as phosphate, Olsen, 1935). For references on tissue-testing methods, see Nicholas (1957).

b. Visual Symptoms (with or without Accompanying Chemical Analysis). The most rapid and convenient method to determine a nutrient deficiency is by observation of visual symptoms, where such occur and are specific enough. In the case of less specific symptoms, as in many conifers, chemical analysis of material graded according to the severity of the symptoms may help to explain the cause of the symptoms. Comparison of unknown symptoms with those of experimental material with known deficiencies is even more essential than in the case of diagnostic tissue analysis. The literature abounds with descriptions of the symptoms of various deficiencies; here reference can only be made to Table I, presenting a number of references containing color plates of deficiency symptoms, and to Table II, listing a number of references describing

TABLE I
PUBLISHED COLOR PICTURES SHOWING SYMPTOMS OF NUTRIENT DEFICIENCIES IN FOREST TREES

Species	Nutrient	Reference
Abies pectinata	N	Hausser (1958)
Chamaecyparis obtusa	P, Mg, Fe, Mn	Tsutsumi (1962)
Cryptomeria japonica	P, K, Ca, Mg, Fe	Tsutsumi (1962)
Picea abies	N, P, K, Mn	C. O. Tamm and Ingestad (1955)
	N, P, K, Cu	van Goor (1963)
	K, Mg	Ingestad (1960a)
	K	Björkman (1953), Themlitz (1958a)
Picea glauca	N, P, K, Mg	Swan (1960)
	K	Heiberg *et al.* (1954), White and Leaf (1957)
Picea mariana	N, P, K, Mg	Swan (1960)
Pinus banksiana	N, P, K, Mg	Swan (1960)
Pinus densiflora	P, K, Mg, Fe	Tsutsumi (1962)
Pinus radiata	N, P, K, Ca, Mg	Purnell (1958)
Pinus sylvestris	P, Mg	Möller (1904)
	N, P, K, Mg	van Goor (1963)
	K, Mg	Themlitz (1958a,b)
	Mg	Brüning (1959)
Pinus strobus	Mg	Heiberg *et al.* (1954), White and Leaf (1957)
Pseudotsuga taxifolia	N, P, K, Cu	van Goor (1963)
Tsuga heterophylla	N, P, K, Mg	Swan (1960)
Robinia pseudoacacia	K, Mg	Brüning (1959)

TABLE II

PUBLISHED WORKS ON TRACE ELEMENT EFFECTS IN FOREST TREES

Element	Species	Experiment in: Field	Laboratory	Symptom as: Deficiency	Toxicity	Growth reduction	Analysis of: Soil	Plant	Method	Reference
Fe	*Agathis australis*		x	x	x	x		x	Solution culture	Peterson (1932a)
	Betula verrucosa		x	x		x		x	Solution culture	Ingestad (1957)
	Fagus sylvatica	x		x		x	x	x	Foliar spray	Olsen (1943)
	Picea abies		x	x		x		x	Solution culture	Ingestad (1959)
	Pinus sylvestris		x	x		x		x	Solution culture	Ingestad (1960b)
	Pinus spp., *Pseudotsuga taxifolia*	x		x		x			Foliar spray	Korstian *et al.* (1921)
	Populus spp.	x		x					Stem injection	Starr (1940)
	Quercus palustris	x		x					Stem injection	Pirone (1940)
	" "	x		x					Fertilizers, leaf treatment	Haeskaylo and Struthers (1959)
	Thuja plicata		x	x		x		x	Solution and sand culture	Walker *et al.* (1955)
Mn	*Agathis australis*		x	x	x	x		x	Solution culture	Peterson (1932a)
	Betula verrucosa		x	x		x		x	Solution culture	Ingestad and Jacobson (1962)
	" "	x		x				x	Foliar spray	Ingestad (1958)
	Juglans regia	x		x					Foliar spray, stem injection	Braucher and Southwick (1941)
	Picea abies	x		x		x		x	Foliar spray, stem injection	Ingestad (1958)
	Pinus radiata		x	x		x			Solution culture	Smith (1943)
B	*Agathis australis*		x	x	x	x			Solution culture	Peterson (1932a)
	Betula verrucosa		x	x	x	x		x	Solution culture	Ingestad and Jacobson (1962)
	Eucalyptus spp.	x		x		x			Fertilizers, foliar spray	Savory (1962)
	Pinus radiata, P. taeda		x	x	x	x			Solution culture	Ludbrook (1940, 1942)
	Pinus radiata, P. patula	x		x		x		x	Fertilizers, foliar spray	Vail *et al.* (1961)
	Pinus radiata		x	x		x			Solution culture	Smith (1943)
	Pinus radiata, P. pinaster	x		x		x		x	Fertilizers, foliar spray	Will *et al.* (1933)
	Thuja plicata		x	x		x		x	Solution and sand culture	Walker *et al.* (1955)
Cu	*Agathis australis*		x		x	x		x	Solution culture	Peterson (1932a)
	Larix decidua, Picea abies, Pinus sylvestris		x	x		x			Soil culture	Rademacher (1940)
	Picea sitchensis	x		x		x		x	Fertilizers, foliar spray	Benzian and Warren (1953)
	Pinus radiata		x	x		x			Solution culture	Smith (1943)
	Populus robusta	x		x		x		x	Fertilizers, foliar spray	Benzian and Warren (1957)
	Pseudotsuga taxifolia	x		x					Fertilizers	van Goor (1963)
Zn	*Agathis australis*		x	x	x	x		x	Solution culture	Peterson (1932a)
	Pinus radiata		x	x		x			Solution culture	Smith (1943)
	Pinus radiata, P. pinaster	x		x		x		x	Foliar spray, stem treatments	Stoate (1950)
	Pinus taeda, P. echinata		x	x		x			Sand culture	C. G. Wilson (1953)
Mo	*Agathis australis*		x	x		x		x	Solution culture	Peterson (1932a)
	Pinus radiata		x	x					Solution culture	Smith (1943)

micro-nutrient deficiencies in forest trees. Many of the references in Tables I and II concern evergreen conifers. Less work has been done on broadleaved forest trees. The symptoms in these trees are often similar to those in orchard trees, so some help can be obtained from the horticultural literature (see Wallace, 1961, and Malavolta *et al.*, 1962, the latter also with data on *Eucalyptus* sp.).

It is thus often possible to recognize at least well-developed nutrient deficiencies in the field by means of visual symptoms, after a certain amount of experience has been gained. In the same way certain toxicities may give recognizably specific symptoms (chloride, sulfur dioxide, etc.; cf. Karschon, 1958). Visual observations can also be utilized in a semi-quantitative way by scoring according to general vigor and color (White, 1958). This method is particularly useful in the assessment of effects of various treatments (fertilizing, thinning, mulching, etc.), where other measurements fail for some reason.

Difficulties in the interpretation of a symptom may arise when a plant suffers from lack of more than one nutrient, or when a deficiency of one nutrient is combined with an excess of another. Van Goor (1963) has described potassium-deficiency symptoms in *Pseudotsuga taxifolia* and *Picea abies* at both high and low nitrogen levels. Such information is particularly helpful and stresses the value of factorial experiments in physiological work.

The amount of chlorophyll—and thereby the color—in the leaves is often considered to be a measure of their nitrogen content. Although this is true in a general way and has been used for evaluation of the nutrient status of nursery stock (Wilde and Voigt, 1952; cf. Mitchell, 1934), it is not always the case (Viro, 1959).

5. INDICATOR PLANT METHODS

a. The Phytosociological Approach. Every plant species has a certain range of physiological conditions over which it can thrive. The range of ecological conditions over which the species actually occurs (at least as vigorous specimens) is usually narrower, because of competition with other plants, damage by parasites or grazing animals, lack of seeds or suitable spots for germination, etc. Nevertheless, the occurrence of many species is restricted to sites with well-defined properties—for example, certain lichens to calcareous rocks, certain plants to soils with a high content of some heavy metals, certain algae to hot springs. In most cases the ecological amplitude is wider, or at least less well defined, but there may still be a good correlation between some habitat characteristics and the occurrence of one or more plant species. Such species are

then called "indicator species," although it is not always clear what they really indicate. It is, however, not uncommon that a species has different soil requirements in different parts of its geographical range.

A practical use of indicator plants in silviculture does not necessarily require that we know exactly what the indicator plants demand; it is clear progress if we, by means of the indicators, can classify the sites into units with different properties concerning actual or potential yield under forest management. Various phytosociological schools have proposed such classifications with considerable success (see *Silva Fennica*, No. 105, 1960). At the present state of knowledge, it is often found that vegetational classifications are more useful than chemical and physical measurements of a more or less complicated nature. On the other hand, there is room for criticism when it is claimed that an indicator plant system gives the answer to questions about causal ecological relationships. Although it is often possible to arrange vegetational units in series according to general trends in supply of water and nutrients, it is by no means proved that a "richer" type of forest area always has a better supply of nutrients than a "poorer," or that a "drier" type has less available water in the profile than a "normal" or "moist" type. The occurrence of the "character species" is determined not only by the site factors of "water" and "nutrients" but also by other factors, in particular earlier development (human influences, forest fire, etc.) and stand density. Moreover, there may be differences in rooting depth between a tree and an indicator plant. A pine may, for instance, exploit deeper soil horizons than the shallow-rooted *Oxalis acetosella*. A further discussion on vegetational units and their relation to the ecosystem concept belongs to the subject of site classification.

Indicator plants may be used for purposes other than in phytosociological connections. The best-known example in forestry is that of the so-called "nitrate plants," a term used by Hesselman (1917) for plants believed to have rather unspecific requirements in most respects but demanding nitrate in the soil to become established and thrive. In addition the nitrate plants accumulate nitrate in their leaves, as evidenced by simple chemical tests. Although the correlation between soil nitrification and the occurrence of these plants (at least as thrifty specimens) appears to be reliable, it seems doubtful whether the causal relationship really is a specific demand for nitrate. Physiological experiments have shown that at least one of the typical nitrate plants, *Chamaenerion* (*Epilobium*) *angustifolium*, grows as well with ammonia as a source of nitrogen as with nitrate (C. O. Tamm, 1956b; Strand, 1957). Yet this group of plants—ecologically somewhat related to agricultural weeds, being weak competitors with high demands for nitrogen and effective seed dispersal—can still be used as indicators of a good supply of nitrogen—for example, that caused by breakdown of mor humus on a clear-cut area. If nitrate is found in the leaves of the nitrate plants, this is of course final evidence of the occurrence of nitrate in the soil. (Nitrate is never found in the leaves of many other forest plants, including trees, apparently because of an effective mechanism for nitrate reduction in the roots.) This kind of information, however, is discussed under the next heading, which deals with indicator plants used as nutrient extractors.

It is also possible to use microorganisms as indicators of the soil supply of nutrients, and *Aspergillus* has been used extensively for molybdenum determinations in arable soils. The reviewer is not aware of any such investigation concerning forest soils, although it has been proved that molybdenum may be a limiting factor for the growth of trees and, still more, for symbiotic nitrogen-fixing organisms (Hewitt and Bond, 1961).

b. Use of "Indicator Plants" for Extraction of Nutrients from the Soil. The difficulties in imitating root activity by chemical agents in soil analysis work have led many investigators to use plants as nutrient extractors. This can be done by pot tests or in the field. The most widely known pot-test method is that introduced by Neubauer (for references, see Bergmann, 1958), in which rye seeds are planted in a mixture of the test soil and quartz sand. The total nutrient content of the rye seedlings is determined after 17 days. The uptake from the soil is then calculated. Tables are available to show the quantities of nutrients that should be available for good growth of various crops. A similar method with tree seedlings as test plants has been used extensively on forest soils by Süchting (references in White and Leaf, 1957). Although this method demonstrates very clearly the great difference in nutrient contents between poor soils and fertile soils (in both forest and arable land), it is doubtful whether it can give a correct picture of the amounts of nutrients available in a forest soil *in situ*, for the same reasons as discussed above under soil analysis and incubation experiments.

It is not always easy, and perhaps not even desirable, to draw a boundary between investigations using plants as nutrient extractors and investigations studying the nutrient requirements of plants. In the important work by Mitchell (for references see Mitchell and Chandler, 1939), both tree species and soils were compared in pot tests.

If the laboratory investigations on extraction of soil nutrients by plants are not sharply separated from physiological tests of nutrient requirements, something similar can be said of tests on extraction by plants in the field in relation to diagnostic plant analysis. It has already been mentioned that nitrate tests on leaves of, for example, *Chamaenerion angustifolium*, *Rubus idaeus*, and *Senecio* spp. can tell us that nitrification is going on in the soil. As there is usually a correlation between nutrient uptake by various plants growing on the same soil, leaf analysis of one species can be used to forecast growth of another species. This could be concluded from the work of Mitchell and Chandler (1939) concerning a number of deciduous tree species. C. O. Tamm (1954) has found a similar correlation between leaf composition in pine, spruce, and birch, and Leyton (1954) has tested the nitrogen contents of *Calluna vulgaris* as an index of suitability of heathland for tree planting. The last type of correlation can prove particularly useful, because there are so few other sources of information on the nutrient regime of sites lacking species of silvicultural interest. The applicability of the estimates obtained is always limited, however, because no two species have exactly the same physiological demands. Other sources of error inherent in the plant analysis method have been mentioned before. Gagnon *et al.* (1958) made extensive analyses of various forest plants without finding evidence for a variation in composition with site properties within each species. Other investigators have obtained more positive results (Höhne, 1963b).

6. THE SUBSTITUTION PRINCIPLE

The first serious attempts to obtain information on forest nutrition were based on the substitution principle; that is to say, for lasting growth the nutrient additions must balance the amounts removed, by harvests or otherwise. Ebermayer (1876, 1882) thus studied the amounts of nutrients contained in various parts of the trees and explained site deterioration after centuries of litter removal as the consequences of destitution with respect to plant nutrients. The lack of experimental evidence, together with the scarce and not entirely reliable data on rain-water composition available at that time, led Ebermayer and his followers to underestimate the role of nitrogen and to emphasize the importance of minerals, among them particularly calcium, which makes up some 50% of many plant ashes (expressed as CaO).

More recently Rennie (1955) has compiled data on nutrient contents in stands and compared them with the amounts in poor heathland soils. He has come to the undoubtedly correct conclusion that many old

heathlands have such small amounts of nutrients within reach of the roots that normal forest growth is impossible without fertilization. Yet it is not quite satisfying to draw such far-reaching conclusions without attempting to make a complete balance sheet for nutrient supplies and losses. The limited annual amounts of dust and rain-water nutrients may become quite considerable during 100 years; at the same time leaching may remove some nutrients (Viro, 1953). Weathering may also be different in a deep-rooted forest as compared with an open heathland.

The comprehensive work of Ovington and his collaborators on dry matter production and nutrients taken up by different tree species is of fundamental importance in this connection (see Ovington, 1962). These and other recent results will be discussed in Section III. Here it should be pointed out that much of the nutrient uptake of plants is "luxury consumption," which does not correspond to a physiological requirement. Instead the various ions in the soil are taken up because the plant has only a limited capacity to distinguish between useful ions and less useful ones. It is thus only as a first approximation that the nutrient content of crops can be used for estimating fertilizer needs.

B. Combinations of Two or More Methods

From the preceding discussion it is clear that no single method other than direct field experiments can give complete and reliable information on the nutrient status of a forest stand, even if there are occasional cases in which this method also gives results that are difficult to interpret. It is, however, usually not economically feasible to make field experiments on the scale required. The question is then: can any combination of the methods discussed above give the desired information more conveniently? The answer to this question is positive, as far as qualitative information is concerned—that is, whether the supply of a certain nutrient is limiting growth. For quantitative determinations of how much growth can be increased by supply of the limiting factor we must always depend on field experiments, even if other information may enable us to draw certain conclusions.

There are several possible combinations of two or more of the six methods discussed in the preceding section; we shall here discuss particularly such combinations that have been used more commonly and successfully.

For a long time (Möller, 1904) pot experiments with seedlings have been combined with observations of symptoms of deficiency or excess. Soon also chemical analysis of the seedlings was taken into account

(Němec, Süchting, Mitchell; for references see White and Leaf, 1957). This approach has been very useful in nursery work, and many of the relationships between visual symptoms, plant nutrient concentrations, and growth have been shown to hold true over a wide range of conditions, including mature trees in forest stands (Walker *et al.*, 1955; Ingestad 1962; Peterson 1962a,b).

We are then already discussing the next combination, that of field experiments in stands together with diagnostic plant analysis, often supplemented also with data from pot or solution culture experiments. The first example of this approach in forestry—and also one of the most successful ones—is the work of H. L. Mitchell and collaborators in the Black Rock Forest during the 1930's. After considerable preliminary investigation a large series of nitrogen dosage experiments was laid out in deciduous forests in the northeastern United States. On these plots were then measured, for each of a number of tree species, the leaf nitrogen concentration in the autumn after treatment and the diameter growth one year later. Both the growth-response curve and the curve for the nitrogen content of the leaves versus nitrogen supply were found to be exponential of the diminishing-return type. Mitchell and Chandler (1939) then assumed that similar leaf nitrogen levels corresponded to similar nitrogen status—that is, that their various curves for leaf nitrogen versus supply from the various series were all parts of the same curve (one for each species), differing only in that each site had its own characteristic output of nitrogen. In fact, they could combine their data into one smooth curve for each species, and thereby obtain a measure of the differences in soil delivery of available nitrogen between the series, expressed in the same units as the applied nitrogen. Furthermore they could establish differences in growth reaction to applied nitrogen between the various species (see below under Section III,B).

It may be said that Mitchell and Chandler overemphasized the importance of leaf analysis as a means of determining *soil* nutrient levels. According to the reviewer's opinion, it is better to concentrate on *stand* nutrient status, which in turn depends both on soil nutrient levels and on other factors. The figures in pounds per acre for soil nitrogen availability obtained by Mitchell and Chandler were, however, not considered by them as anything but relative measures. A further example of this relativity is the observation by C. O. Tamm (1956a) that soil nitrogen availability (= the constant b in the Mitscherlich equation) may be different for dominant and for more or less suppressed trees in the same stand. Nevertheless the approach of Mitchell and Chandler is one of the great advances in forest nutrition work.

Several later investigators have tried to standardize their leaf analysis data by means of field experiments, with or without additional pot experiments, essentially in the same way as Mitchell and Chandler (Leyton, 1958b; Heiberg *et al.*, 1959; Gessel, 1962; Wehrmann, 1963a; C. O. Tamm, 1956a, and in press, a). The use of the exponential curve has not been so common; instead there is a trend to use multiple correlation methods in the interpretation of both experimental and nonexperimental data (Leyton, 1958b; Wehrmann, 1963a; C. O. Tamm, in press, a). In this connection it should be particularly emphasized that generalized conclusions about standard values (e.g., optimum levels) can be drawn only from carefully controlled experiments and samplings. Both leaf composition and growth must be measured at the right time (which is not necessarily the same time for each). An experimental treatment changes both composition and growth, and the time courses of both processes are often not the same; usually the concentrations recede faster than growth. Whether optimum ranges narrow enough to be useful in diagnostic work actually exist is a matter of discussion. Evidence has been advanced corroborating the assumption of relative constancy in optimum ranges over widely varying conditions (Mitchell and Chandler, 1939; Leyton, 1958b; Ingestad, 1962), but some authors (Leyton, 1958b) hesitate to accept it as a general conclusion. The definitive answer, which may be different for different species, can be given only by further experiments, preferably of the factorial type. Table III, based on Ingestad's data, gives optimum ranges suggested for several elements in species of pine, spruce, and birch (cf. Ingestad, 1962; Ingestad and Jacobson, 1962; Leyton, 1958a).

Although opinions are thus somewhat divided regarding the nature and value of optimum levels (whether expressed as percentages of dry weight, as quotients of two nutrient concentrations, or otherwise), there is a fairly general agreement that deficiency levels in nutrient concentrations can be established and used for diagnostic purposes. Several authors have published tables for deficiency levels in various trees (Leyton, 1958a; C. O. Tamm, 1956a; Ingestad, 1962), although different criteria for deficiency have been used, such as "region of minimum" (Mitchell and Chandler, 1939), 50% of optimum growth (Ingestad), or simply the occurrence of a definite growth response (C. O. Tamm). Some data are also available for nutrient levels at incipient deficiency symptoms (Swan,

1960; Ingestad, 1962; Peterson, 1962a,b; see also references in Tables I and II). In the case of deficiency levels there also seems to be a remarkably good agreement between most species and investigators (see Ingestad, 1962, concerning some of Mitchell's data). A comparison can here also be made with orchard trees (Goodall and Gregory, 1947).

TABLE III

Optimum Concentrations and Concentrations Corresponding to Visual Deficiency Symptoms in Leaves of *Pinus sylvestris*, *Picea abies*, and *Betula verrucosa*[a]

	Percentage of dry weight in:					
	Pinus		*Picea*		*Betula*	
Element	Optimum	Deficiency	Optimum	Deficiency	Optimum	Deficiency
N	2.4–3.0	0.7–1.6	1.8–2.4	1.0–1.7	3.4–4.0	1.5–3.1
P	0.15–0.4	0.06–0.09	0.10–>0.3	0.05–0.11	0.2–0.4	0.12
K	0.9–1.6	0.3	0.7–1.1	0.3	1.5–3.1	0.5
Ca	0.04–0.3	0.05	0.09–0.6	0.02	0.16–0.6	0.12
Mg	0.12–0.18	0.06	0.09–0.16	0.02–0.07	0.17–0.5	0.06–0.18
S	0.20–0.25	0.07	0.13–0.18	0.13	0.29–0.32	0.06–0.21

[a] Data from Ingestad (1962). Material from solution culture experiments at relatively low light intensity.

It is thus clear that diagnostic plant analysis combined with experiments in the field, or both in the field and under controlled conditions, forms a very useful approach in forest nutrition research, although the present author prefers to call leaf analysis a semiquantitative method for classifying stand nutrient status in the sense that the information obtained is not very accurate. The grading of sites by means of plant analysis is thus permissible only under particularly favorable conditions, one of which is sampling under similar climatic conditions.

It may now be asked whether it is possible to combine soil analysis with field experiments and get a similar amount of information as with foliar analysis and field experiments. This is the most widely used approach for determining fertilizer demands in agriculture in most countries. The answer is that no logical reasons prevent the establishment of standard soil values for good growth and the determination of amount of fertilizer needed after the actual soil values. This has also been done from time to time for forest nursery crops (Wilde, 1958). Certain levels of soil properties have also been suggested as guides for fertilizer demands

in the field—for example, 2.2% nitrogen in a mor humus as an upper limit for a nitrogen response (Wehrmann, 1963b). Absolute or relative amounts of potassium (Heiberg *et al.*, 1959) and phosphate (van Goor, 1956a; Baur, 1959) have also been used as more or less well-established deficiency limits.

To these statements could be added numerous others concerning the investigations which so far have failed to show clear correlations between soil analysis and experimental results. There is no need to repeat here the reasons why soil analyses are sometimes difficult to interpret in relation to crop responses, particularly with deep-rooted plants such as most trees.

It was pointed out earlier that one of the weaknesses in the "substitution principle" was the possibility of luxury consumption of nutrients by the crop. If experimental evidence (or foliar analysis referring to experimental standard values) makes it clear that one or more nutrients limit growth on the plots in question, a total analysis of the crop for this or these elements gains much in interest, particularly if the results can be compared with the total contents in the soil. Of even greater interest than the total amounts contained in the crop is the annual turnover. The litter-fall is often taken as an approximation of this figure, sometimes with a correction for root "litter." Soluble substances washed from the crowns should also be taken into account in the case of, for instance, potassium (Madgwick and Ovington, 1959). In the correct use of the substitution principle other factors must also be considered: losses by leaching, volitilization (NH_3 from soils with a high pH, SO_2), or denitrification, gains by weathering, nutrients in rain water or dust, nitrogen fixation. This is not always possible, but still it is of great importance for practical forest fertilization to know what amounts of nutrients are contained in a forest stand. The stand cannot be expected to take up more than a fraction of its original content if a single dose of an easily soluble fertilizer is supplied (Heiberg *et al.*, 1959; Wittich, 1958; Heilman and Gessel, 1963a; C. O. Tamm, 1963).

The indicator plant methods can of course also be combined with other methods; in fact, it would be most desirable to find out more about the requirements of various indicator species. Both physiological experiments and field experiments are called for. Of interest are not only the demands for nutrients, water, light, etc., but also the ability of the "indicator species" to germinate and colonize, their ability to survive under unfavorable conditions, their sensitivity for competition, etc.

Regarding methods of determining available nutrients by plant

uptake in pot cultures, it is the author's opinion that they can be very useful in physiological studies of the differences in root activity of both indicator plants and various indicator species, but that they may be misleading if considered as bioassay methods for nutrients. They should then at least be supplemented with other sources of information, such as trenching experiments in the field, which may tell whether nutrient mobilization is much changed by cutting off the tree roots.

III. Critical Discussion of Some of the More Important Results of Forest Nutrition Research

A. Differences in Nutrient Status between Trees Growing under Different Conditions with Respect to Competition, Age of Stand, and Human Influences

It has already been pointed out that seedlings need a more steady supply of nutrients than adult trees and therefore may appear more demanding. It is an open question as to what extent internal nutrient requirements change with age. It is difficult to solve this question by comparing the results of experiments with fertilizers applied to stands of various ages, including newly established plantations, because young saplings and big trees do not live under the same conditions, not even when they are growing together. In the latter case the saplings live in the shade of the overstory, which means higher humidity, less light for photosynthesis, and often a change in the shoot-to-root ratio, impairing the development of the nutrient- and water-absorbing system.

Both the saplings and the big trees may be growing on soils that were previously identical—for example, heathland or arable land—but as some decades under a specific kind of forest cover may change soils very considerably (Ovington, 1962) they may no longer be comparable. This difficulty is commonly circumvented by comparing old stands with young growth established after clearing part of the old forest (Höhne, in press). This is, however, not always better than other alternatives, because clear felling means a very radical change in the nutritional situation of the site. All or most competition for light, nutrients, and water is suddenly removed, unincorporated organic matter on the soil surface is exposed to very different conditions, and much fresh organic matter (leaves, twigs, roots, mycorrhizal fungi) is made available to the organisms of decomposition. The last factor has been particularly stressed by Romell (1935, 1957), who called the nutrient liberation resulting from felling the "assart effect." This phenomenon has been known, although

not understood, by man since ancient times. Most primitive agriculture uses some system of "shifting cultivation" in which the assart effect is the factor responsible for the relatively high fertility of sites not capable of giving annual harvests without manuring.

It is necessary to take the assart effect into account not only on clear fellings but also in connection with other silvicultural treatments in which part of the trees or vegetation is killed—thinning, removal of scrub with phytocides, slash burning, etc. A five-year series of samplings from ten variously thinned spruce plots in southwestern Sweden (C. O. Tamm, in press, b) has shown a clear trend to lower nitrogen levels on the "self-thinned" plots in comparison with the actively thinned plots. Of course, the number of stems and the green weights of the stands are higher on the "self-thinned" plots, so part of the difference in nitrogen levels may be ascribed to differences in competition. It has been demonstrated, however, by Romell (1938) and others in trenching experiments in closed stands that cutting off the tree roots provokes changes in vegetation and humus very similar to those occurring on clear fellings. This means that ordinary thinning must also affect the nutrient regime.

The difficulties in demonstrating the possible differences in nutrient requirement between old and young trees must not discourage future investigations. It is very important to gain more knowledge about the relations between tree growth, physiological aging, and soil nutrient supply. In fact, it has been suggested that the well-known decrease in forest yield at advanced ages is caused more by nutrient deficiency (Romell, 1957) than by physiological aging or respiration losses. In old stands on poor sites, a considerable part of the nutrients of the site may be bound up either in the trees (Rennie, 1955; Ovington, 1962) or in an "inactive" mor layer (Hesselman, 1937).

The concentration of nitrogen in needles from stands growing very well is often relatively low. (Mitscherlich and Wittich, 1958; Strebel, 1961; C. O. Tamm, 1963), but it would be premature to take this as evidence for a lowering of the optimum levels with age. Tamm got only a small response to nitrogenous fertilizers; on the other hand, Mitscherlich and Wittich obtained a larger response at similar or somewhat higher foliar levels. In some cases discrepancies between response and foliar levels near the apex may be explained by a difference in composition between apical leaves and the bulk of the crown (cf. Zöttl and Kennel, 1963), but this is not likely in Tamm's case where samples from whole crowns of felled trees were shown not to differ much from samples taken near the apex.

Responses to fertilizer applications are common in forests where human influence has modified soil and stand. A particularly severe influence has been the litter removal practiced in Central European forests for centuries. Sites subject to this treatment several times are often deprived of most of the nitrogen accumulated under earlier forest generations. Also wetland drainage, which improves soil aeration and organic matter turnover, may have adverse side effects by cutting off earlier sources of nutrients (with flooding water). Managed forests, often with introduced species, may grow faster than virgin forests and therefore require more nutrients, (see also Section III,C).

B. Differences in Nutrient Requirements between Species

The differences in nutrient requirements between different tree species have often been discussed rather loosely on the basis of field observations (the phytosociological approach, sometimes supplemented with soil analysis). Many investigators have carried out culture experiments, however, either in the field or under laboratory conditions. Most field experiments for this purpose consist in plantings at different but not very well-defined fertility levels. The field experiments can be extended to higher ages. This is a great advantage compared with pot or solution culture experiments which do, however, admit better defined nutrient levels and a more complete physiological analysis of the growth measurements (e.g., Mitchell, 1934; Ingestad, 1962). Mitchell and Chandler (1939) made an attempt at physiological analysis of nitrogen requirements, based on leaf analysis data from fertilized field plots, and separated a number of deciduous tree species as "nitrogen-demanding," "intermediate," and "nitrogen-deficiency tolerant." The decisive characteristic of the species, according to Mitchell and Chandler, is its ability to maintain a level of nitrogen in the foliage, which is high in relation to its optimum level, even on soils with low nitrogen availability.

Ovington (1962) later pointed out that the nutrient uptakes of different species, planted as pure stands on the same site, are governed mainly by the amount of growth under the circumstances. Differences in chemical composition of the trees play only minor roles in the nutrient consumption of the stand. Yet Ovington's results tell us nothing about what would happen if the nutrient supply of the site were changed. It seems probable that some of Ovington's faster-growing species were closer to their nutrient optimum than were some of the more slowly growing ones.

Ingestad (1962) found that he could not use the criterion of Mitchell and Chandler for nitrogen demand in his comparisons of pine, spruce, and birch in solution culture. The foliar nutrient level, measured in relation to the optimum range in the three species, was not very different if only small amounts of nitrogen were supplied, but the growth of the pine seedlings on these low amounts was considerably better than that of spruce and birch. His results seem to indicate that general statements on higher or lower nutrient requirements of various species may be rather misleading. In each comparison both the physiological function for which the nutrients are required and the conditions under which the comparison is believed to be valid should be stated.

In field research, attention must be paid not only to the physiological demands of different species but also to their ability to satisfy these demands under field conditions. As mycorrhizae seem to play a very important role in the nutrient uptake of forest trees, the physiological behavior of mycorrhizal fungi is of great interest. The dependence of the mycorrhiza on soil conditions and on the light supply to the host has been studied by Hatch, Gast, Björkman, and others (for references see Handley, 1963). The low light supply to the understory in a forest may mean that the frequency of mycorrhizal roots is low, and consequently the ability to compete for nutrients is decreased.

The best approach to the study of ecological nutrient requirements of various species is still, in the opinion of the author, that used by Mitchell and Chandler, a combination of extensive field experiments with foliar analysis.

C. Differences in Nutrient Status between Stands Growing in Different Regions and on Different Substrates

1. SOME REMARKS ON THE GEOCHEMICAL BACKGROUND TO DIFFERENCES IN SOIL NUTRIENT SUPPLY

Local variations in site fertility are among the most studied aspects of forest nutrition. Regional variations have received considerably less attention, even if some valuable observations have been made. Yet many of the known relationships between site properties and forest yield can still be considered only as statistical correlations, while the causal explanations are more or less obscure. In the author's opinion more systematic thinking about "factors forming the nutritional situation," by analogy with the pedologist's treatment of "factors of soil formation"

(Jenny, 1941; cf. Major, 1951), would be desirable. An appropriate starting point would be a study of the geochemical aspects of the forest nutrient cycle. The following pages are no attempt to review this particular subject but may help to demonstrate the need for this approach. The reader may find some further information in the limnological review by Gorham (1961).

If we consider the nutrient cycle of a virgin forest, we find that tree growth is usually well adjusted to the natural supply of nutrients from litter decomposition, weathering, "flush," and atmospheric additions. Such an adjustment is rare in agriculture (it is most apparent in periodically flooded areas—for example, since ancient times in the Nile valley). Exceptions from this relative equilibrium between nutrient uptake by organisms and release from dead organisms can be found in certain wet or cold forest types where decomposition is hampered. Growth and nutrient uptake are usually also retarded, however. In all humid areas there is a loss of soluble salts in runoff water (Viro, 1953). An equilibrium requires that this loss be compensated for; this can result from either weathering or atmospheric supply, if we restrict the discussion to sites not influenced by "flush." As we know that many sites have carried forests continuously for many thousands of years, there must be such a compensation. The large differences in forest yield between sites with different parent material suggest that weathering is an important factor, at least in regions with, geologically speaking, "young" parent material. In large areas with "old" parent material in regions with a warm or hot climate, weathering may have proceeded so far that the further amounts of nutrients that can be released are very limited. Time thus comes in as a factor, as in Jenny's list of soil-forming factors. The atmospheric supply may become very important when weathering intensity is low (Gorham, 1961). In the case of nitrogen, atmospheric supply is probably important in all regions, although it seems necessary to presuppose some regions where more nitrogen is lost to the atmosphere than is gained from it, because much atmospheric ammonia appears to be of terrestrial rather than marine origin (Eriksson, 1952).

We have now discussed, or at least mentioned, several factors affecting the nutrient supply to a site, as well as the nutrient losses from the site. In the first group we have (1) weathering, (2) "flush," and (3) atmospheric supply (by rain water, dust, direct absorption, biological fixation). In the second group we have discussed (1) leaching. Other processes possible are (2) denitrification (and loss of gaseous ammonia from alkaline soils); (3) soil erosion, as after a forest fire, when both water and wind erosion may occur; (4) fixation of nutrients in soil minerals, which over shorter periods may be considered as a minus in the nutrient balance although it counteracts leaching; and (5) "biological fixation" of nutrients in living organisms and their remains, which also counteracts leaching, though to a highly variable degree.

In the preceding paragraphs we have discussed only virgin forests. In managed forests we have also to consider (6) nutrient losses with harvested forest products (Section III,A); under certain circumstances other phases of the nutrient cycle are also affected (for example, by litter removal). (7) Nutrients in lesser vegetation may be consumed by grazing animals, which only partly compensate for the removal by their droppings. (8) Leaching and soil erosion is often increased by man, as in connection with prescribed burning. (9) "Flush" effects may be cut off by draining operations. (10) Both weathering and atmospheric supply may depend on the composition and amount of vegetation, which is often changed by man. (11) The rate of turnover of the soil organic matter may be greatly increased by soil working and other treatments (for instance, in connection with plantation treatments or, more especially, shifting cultivation). (Treatments such as liming or fertilizer application are considered as outside the present discussion.)

The geochemical aspect comes in very clearly when the effects of all these processes are summed up for the various elements. The differences between the elements are great. A short discussion concerning some plant nutrients will show this.

Nitrogen. All nitrogen within a forest ecosystem is usually considered as originating from the atmosphere (Ovington, 1962). There are annual additions of ammonia and nitrate in the precipitation. There may also be a direct absorption of ammonia from the atmosphere, but this is of unknown importance (cf. C. O. Tamm, 1958). Fixation of molecular nitrogen by free-living or symbiotic organisms is important in certain forests (for example, alder forests) but does not seem to play any great role in other types, such as acid coniferous forests (Laatsch, 1961). The main losses of nitrogen are by leaching (nitrate, some ammonia, and some organic bound nitrogen; Viro, 1953) and denitrification (Laatsch, 1961). The leached nitrogen contributes to the fertility of "flushed" sites and also to the usually high nitrogen content of low moor peat. Eventually part of this nitrogen follows the rivers into the sea. Sites with a rich supply of mineral nutrients are generally believed to be also richer in

nitrogen than are poorer sites, if the moisture regimes are comparable. This correlation is at present not quite understood, but differences in stability of humus substances formed at high and low base-saturation and the effect of clay minerals on the stability of humus may offer some clues.

Phosphorus. Phosphorus and nitrogen follow each other in the "inner cycle" within the ecosystem but behave very differently geochemically. Phosphorus compounds are much less readily leached away than are other plant nutrients; very little phosphorus is supplied from the atmosphere, presumably mostly as dust (rain-water analyses as a rule concern filtered samples and are therefore incomplete). For these reasons most peatlands are low in phosphorus. The same holds true for many sandy sediments. Limestones also may be low in phosphorus; in addition their high pH makes the phosphate less available. Phosphorus is often a limiting factor in lake and sea water.

Potassium. Potassium is much more common in the earth's crust than phosphorus and nitrogen. It is contained in many minerals, both easily weathered ones (mica) and more resistant ones (feldspars). It is also a constituent of secondary clay minerals, where it can, however, be exchanged with other ions (easily when adsorbed, slowly when incorporated into the lattice). The potassium supplied by precipitation and dust exceeds that of phosphorus but is not very large. On light sandy soils and on peats a large part of the ecosystem's potassium may be biologically fixed—that is, bound to living organisms and their remains. Under these circumstances it is easy to understand that a pronounced potassium deficiency may be induced by temporary cultivation or by peatland drainage (which cuts off "flush" and increases demands for potassium).

Calcium. Calcium is usually the dominating metal cation in the soil solution and on the colloids, even on sites with a "lime-free" parent material and low base-saturation. The reason is the common occurrence of calcium in many minerals, as well as in atmospheric dust. Many forest trees have limited calcium demands (Table III), and their physiological requirements for calcium are fulfilled on most sites. Some soil organisms may require higher calcium or base-saturation levels than do the trees. In certain cases the soil balance between the various ions is abnormal—for example, where the parent material is serpentine or phyllite, rich in magnesium and potassium, and low in calcium (Wittich, 1956). Pronounced calcium deficiency of this kind appears, however, to

be a rather local phenomenon. Unbalanced saline soils are usually not forested.

Sulfur. Sulfur is supplied in considerable amounts from the atmosphere, as sulfate of marine origin and as sulfur dioxide of volcanic origin as well as from combustion of coal and oil. Before industrialization this latter supply must have been lower. Sulfates are easily leached away, which explains why high-yielding agricultural crops may need sulfur fertilization, in spite of the atmospheric supply. Sulfur deficiency seems rather uncommon in forest stands.

Other Elements. Magnesium and boron both occur in sea water in quantities of ecological interest for land plant nutrition after transport by windborne sea spray. Other important sources are weathering (Mg), and volcanism and combustion (B). The main sources of heavy metals are terrestrial. Original rock composition seems to be a dominant factor in most cases with regard to total amounts of these nutrients, but the availability is to a large extent controlled by pH, redox potentials, chelating organic substances, and soil texture. Some micronutrients, iron in particular, are common in dust (for references see C. O. Tamm, 1958).

2. EXAMPLES OF REGIONAL AND LOCAL DIFFERENCES IN FOREST NUTRITION

Responses to application of nitrogen, but no responses or small responses to other nutrients, have been reported for a number of representative sites within the northern conifer belt (Fig. 1; Gessel, 1962; C. O. Tamm and Carbonnier, 1961). Tsutsumi (1962) and others have reported strong effects of mixed fertilizers in Japan; foliar composition suggests deficiency in nitrogen. Conifers in some areas south of the conifer belt proper may also respond in the same way (Wehrmann, 1963b). The deciduous hardwoods south of the "taiga" type of forest have not been so much studied, but Mitchell and Chandler (1939) also demonstrated the occurrence of widespread nitrogen deficiency in some of these woods. Many of the sites where nitrogen scarcity has been demonstrated have been deteriorated by man, but virgin forests in Sweden (Hesselman, 1937; C. O. Tamm and Carbonnier, 1961) have shown similar reactions. Drained peatlands have responded to phosphorus, potassium, nitrogen, and occasionally to manganese (see the review by Heikurainen in this volume).

On mineral soils in western and middle Europe the nutritional situation appears to be more diversified than further north. It has already been mentioned that nitrogen responses occur, and most practical forest

fertilization aims at an improvement of the nitrogen nutrition, although indirect means are often used (lime and phosphate application, introduction of lupines). There are, however, an increasing number of cases being established in which scarcity of phosphate appears to predominate over the nitrogen deficiency (Hausser, 1950; van Goor, 1956a, 1963; Guinaudau, 1959; Holstener-Jørgensen, 1963). Potassium and magnesium deficiencies have been reported from sandy soils (often depleted fields) in both North America (Heiberg *et al.*, 1954; Lafond, 1958) and Europe (van Goor, 1956b; Brüning, 1959). Copper deficiency has occasionally been met with in the Netherlands (van Goor, 1963) and in Britain (Benzian and Warren, 1956). It has been shown that productive natural stands on young and relatively unweathered soils in Switzerland hardly respond to fertilization (Leibundgut and Richard, 1957), in contrast to the high-yielding spruce stands studied by Mitscherlich and Wittich (1958). Holmes (quoted by Ovington, 1962) found no immediate response to N, P, K, Ca, and Mg in pole stage stands of conifers in Britain.

Whereas nitrogen supply seems to be the first controlling factor for the current growth in a considerable part of the forests in Europe, North America, and Japan, phosphorus appears to be the key element in many sites in Australia and New Zealand (Stoate, 1950; Weston, 1958), even though nitrogen deficiency has also been met with there (Peterson, 1962b). Scarcity of zinc is often associated with phosphate deficiencies in Australia; cases of molybdenum or boron deficiencies have been reported from New Zealand (Peterson, 1962b; Will *et al.*, 1963). The chemical composition of the soil parent material rather than unavailability appears to be the cause of these deficiencies.

Very little is known about the forest nutrient situation in tropical countries. Research there has just started, and in several countries information is available on the amounts of nutrients in stands and soils (see references in Ovington, 1962). It is thus the "substitution principle" that has been used for the first approach, as earlier in Europe. Experiments have been carried out only occasionally, where reforestation work has failed for some reason (Savory, 1962; Vail *et al.*, 1961). The cited studies have revealed a boron deficiency in East Africa, said to be widespread also in agricultural crops in the same areas. It is a difficult question to decide to what extent the growing knowledge of the nutrition of cultivated tropical trees such as rubber or oil palm may be applied to forests.

Occasional studies have been made on Mediterranean forest trees (Oppenheimer and Halfon-Meiri, 1961), but it seems premature to draw any general conclusions.

D. Some Problems Worthy of Particular Attention and Some Remarks on the Importance of Further Research

1. Investigations on interactions between soil nutrients and other factors, especially water supply and temperature

We have so far discussed the determination of the nutrient requirements of forest trees and the nutrient status of forest stands as a separate problem, even if it has been made clear that nutrient requirements and nutrient status are relative entities, which may change when other environmental conditions vary. If our studies are to merit the designation "ecological," we must always consider the interactions between the various parts of the environmental complex. Soil drought or lack of oxygen in the soil as well as low temperatures may check the decomposition processes and thereby nutrient availability. In some cases this will be compensated for during periods of more favorable conditions; in other cases the soil processes will lead to accumulation of partly decomposed organic matter or to a loss of nutrients by leaching or denitrification, because decomposition takes an "unfavorable" course (no formation of stable humus) or because it takes place at periods when the root activity is low. There are numerous reports on the influence of temperature on ion uptake by roots, suggesting an increasing difficulty in taking up at least anions in cold climates. This may or may not be compensated for by an increased number of absorbing organs (root hairs or mycorrhizal hyphae). Soil moisture stress both reduces nutrient uptake (Danielson and Russell, 1957) and, through its depressive effect on growth, reduces to insignificance growth response to applied nutrients such as nitrogen (Musick *et al.*, 1963). The water stresses which develop in the plant as a result of soil water stress severely reduce the translocation and redistribution of nutrients (A. M. Wilson and McKell, 1961). Unfortunately, however, little work on the interactions between water stress and nutrient supply has been done with trees.

The reviewer emphasizes the importance of basic studies for our understanding of the relationships between plant nutrition and productivity. In addition to studies on ion uptake and availability as just discussed, investigations of the influence of the nutrient status on physio-

logical processes such as photosynthesis (for references see Keller, 1962), respiration, transpiration, translocation, and hormonal regulation would be particularly welcome.

2. THE STUDY OF THE NUTRIENT STATUS OF IMPORTANT PARTS OF THE WORLD'S FORESTS

As outlined in Section III,C, there are important blanks in our present knowledge of the nutrient situation of the larger part of the world's forests. Gross photosynthetic production is higher in tropical rain forests than in most other types of vegetation, although it is a matter of discussion whether the annual yield is correspondingly high. Yet very little is known about the nutrient situation, except that the amounts of nutrients in the tree stand may be very high (Greenland and Kowal, 1960). The soils are often considered to be very low in both total and available nutrients, although analyses have been presented showing that this is not always so (Cunningham, 1962). Further studies, preferably by experimental methods, are highly desirable on the nutrition of humid tropical forests.

In many cases, in both tropical and temperate countries, strong differentiation occurs between dry and moist seasons. Under such circumstances soil physical properties are decisive for forest yield and often also for the survival of trees and reforestation. Nutritional questions are in such cases often considered to be of secondary importance. Although this may be true in many cases, there are indications that well-nourished trees may survive and grow better than trees with an unbalanced nutrient status. Here, also, more research is called for.

Although something is already known about the nutrient situation in temperate forests of both hemispheres, many problems still await their solution. Only the rough outlines of the nutrient cycle are known. There are also large blanks in our knowledge concerning the importance of various soil processes for tree nutrition.

3. CONCLUDING REMARKS: THE NEED FOR A BETTER KNOWLEDGE OF THE ROLE OF NUTRITIONAL FACTORS FOR THE ACTUAL AND POTENTIAL YIELD OF FORESTS AND OTHER VEGETATION THE WORLD OVER

The standing crop of the world's forests represents a capital of enormous value, even in countries where the main use of the forest is to serve as fallow in the practice of shifting cultivation. The annual growth of the forest is increasing in value in all countries. Management in accordance with regular silvicultural systems is replacing exploitation

of virgin forests, and it is becoming more and more urgent to know not only the actual yield on a site but also the potential yield, if other and more economic species are to be introduced. Objective foundations for planning in forest policy will be more and more indispensable in the future, even if at present the experience of trained foresters, collected by the principle of trial and error, is often worth more than any number of chemical analyses of soil and foliage.

It has been common to consider the climate as by far the most important factor for forest growth (Paterson, 1961); next to climate, soil physical properties are often mentioned (Coile, 1952). Although these statements may be true in a general way, there is no doubt that under some circumstances variations in soil nutrient supply may more than compensate for the effects of the other two factors. The lack of success of some attempts to use climatic indices to predict actual yield may be explained in this way. The dramatic responses to phosphate in parts of Australia and New Zealand are also good examples, and even if such extreme effects are less common, more "normal" responses are enough to warrant further investigations on forest nutrition. The practical application of fertilizers is not necessarily the goal for this research. It seems even more important that we learn *why* some sites are better than others, and *why* some tree species yield more than others on particular sites.

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